Emergence and extinction of the Givetian to Frasnian bryozoan faunas in the Kostomłoty facies zone, Holy Cross Mountains, Poland

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Devonian bryozoans have been investigated from two Givetian to Frasnian localities in the Holy Cross Mts (Central Poland), representing fossiliferous ramp slope facies of the Kostomłoty facies zone (north-western periphery of the Kielce carbonate platform). Thirteen genera belonging to four families and three orders have been identified. Bryozoans show close relation to previously described Givetian and Frasnian bryozoan faunas of France, but also some affinities to easterly regions (e.g., Kuzbass). The main immigration episodes are related to late Givetian and middle Frasnian deepening pulses. The replacement of locally rich and diverse Givetian carbonate bank faunas by overall impoverished Frasnian reef-complex associations largely corresponds to a major extinction event in the evolutionary history of Bryozoa. Five new species are described by I. Morozova and O. Weis: *Eridotrypella arguta*, *Eridotrypella exserta*, *Eostenopora nimia*, *Primorella nitida*, *Primorella indigena*.

Key words: Bryozoa, Devonian, Givetian, Frasnian, taxonomy, biogeography, Poland.

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Introduction

Suitable Devonian exposures in the Holy Cross Mountains, Central Poland (Fig. 1), were palaeontologically and biostratigraphically studied since the second half of the 19th century, but the knowledge of the bryozoan faunas is scarce. This fossil group was a minor component of many benthic, mostly brachiopod-rich or reef-related assemblages; even though several taxa were noted in many studies (especially in Gürich 1896; see also Sobolev 1909; Czarnocki 1950; Baliński 1973; Racki et al. 1985, among others), fragmentary systematic investigations are limited to fossiliferous, clayey to marly Middle Devonian strata of the northern, Łysogóry Region as yet (Kiepura 1965, 1973). The thick, Givetian–Frasnian carbonate succession of the more shallow-water southern (Kielce) Region was recently comprehensively studied palaeobiologically (see summary in Racki 1993), but bryozoans are essentially the only common fossils waiting for refined investigations.

A fairly rich bryozoan collection was gathered during the previous stratigraphical works, and the principal objective of the present paper is a taxonomical analysis of the collected material from two most fossiliferous sites in Kielce Region, late Givetian to middle Frasnian in age. The sections sampled are located in the north-western periphery of Kielce carbonate platform (Figs. 1B and 2), delineated as the distinct Kostomłoty facies zone by Racki (1993). Even though a tentative comparison is given with more sparse late Givetian bryozoan faunas from southerly localities (Kowala Formation), this will be a goal of separate study. Fifteen taxa identified and mostly figured herein comprise as many as five new species, and a close biogeographical links with the Western Europe and a regional record of the Givetian–Frasnian bryozoan turning point are documented.

Palaeogeographical and stratigraphical setting

Devonian strata of the Holy Cross Mountains belong to the elongated belt between south-western margin of the East European Craton and Variscan Deformation Front. The shelf, up to 600 km in width, formed South Polish to Moravian fragment of pericratonic basin stretching from Western Europe to Ukraine along the periphery of the "Old Red Sandstone Continent" (Laurussia; see Fig. 1A). The Middle to Upper Devonian epicontinental succession over the shelf indicates continuous but punctuated drowning of an increasingly differentiated vast stromatoporoid-coral platform (*Stringocephalus* bank) which terminated in the Visean (see e.g., Racki 1993; Szulczewski 1995). There is an overall accordance of the rec-

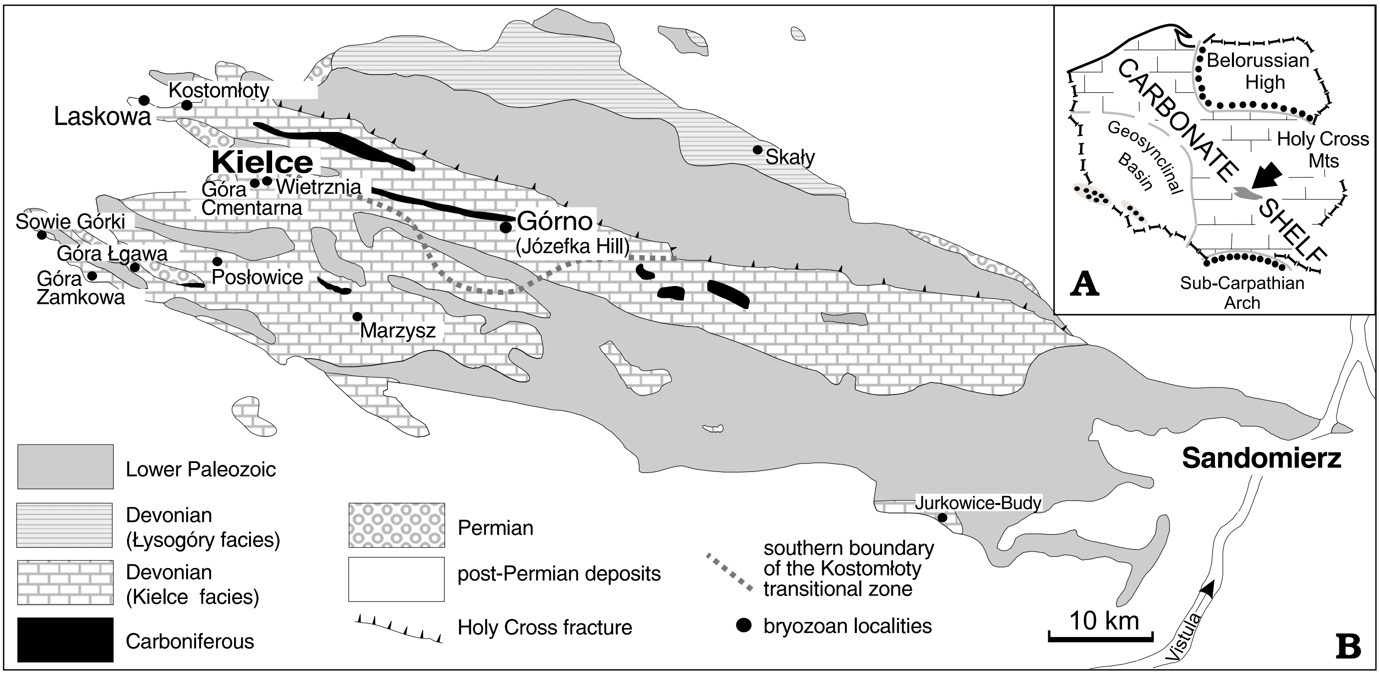

Fig. 1. Location of bryozoan sites in Poland (**A**) and Holy Cross Mountains (**B**, based on Racki 1993: fig. 2); see also Fig. 2 for palaeographic-facies setting.

ognized events with the Euramerican sea-level curve of Johnson et al. (1985). Two distinct palaeogeographic-tectonic facies domains of the Holy Cross area (the Kielce palaeohigh and Łysogóry palaeolow; Fig. 1B), coupled with transitional Kostomłoty area (Racki 1993), offer an opportunity to compare the record of faunal events in several sedimentary regimes (Fig. 2). The subsymmetric facies plan is shown by the central location of the Frasnian Dyminy Reef, surrounded by drowned, poorly-oxygenated deeper-shelf areas (= intrashelf basins): Chęciny-Zbrza (southern) and Łysogóry-Kostomłoty (northern), as summarized in Racki (1993) and Szulczewski (1995).

Among not very numerous bryozoan localities (for details of locations see "Register of localities" in Racki 1993), only two most productive sites from the Kostomłoty zone are studied thoroughly here (Figs. 1B and 2). The westerly locality, Laskowa Quarry, yielded a rich but not very differentiated fauna (four taxa) from the upper Givetian (Middle *Polygnathus varcus* to *Klapperina disparilis* zones) limestones and marls, dominated by tabulate coral (*Coenites*) biostromal to biohermal deposits with many and brachiopod-crinoid partings (Laskowa Góra Beds; Racki et al. 1985; Racki 1993). Approximately coeval, more diverse association (nine taxa) is derived from the fossiliferous, partly biostromal marly set A at Józefka hill near Górno (set B of Małkowski 1981), the most productive bryozoan locality in the Kielce Region. It is followed in the sequence by middle Frasnian fistuliporid-rich fauna in detrital-marly strata distinguished by characteristic thin crinoid and coral-stromatoporoid detrital intercalations (a variety of middle Wietrznia Beds; set C in Racki 1993). This bryozoan-enriched interval is thought herein to represent *Palmatolepis punctata* Zone, but its boundaries are weakly constrained in the poor outcrop, and partial assignment of the set C to the *Palmatolepis transitans* and *Palmatolepis hassi* zones is possible as well (see also Małkowski 1981).

Comparative bryozoan taxa were derived from the southern part of the Kielce (stromatoporoid-coral) facies domain, corresponding to bank-to-reef succession (Kowala Formation, Fig. 2; see Racki 1993). Oldest scarce data come from the middle and upper parts of the Givetian *Stringocephalus* Beds, whilst more diverse associations are found in the uppermost Givetian limestone-marly Jaźwica Member and lower Chęciny Beds (see Fig. 2 and Table 1). Summarizing, the bottom-level bryozoan faunas under study come from various open-shelf, ramp slope and intershoal facies, whilst more shallow-water and reef-related associations still await a systematic study.

Material

The collection studied consists of about a hundred colonies in a different state from preservation, recovered mostly by washing of fossiliferous marl-shaly deposits; for compact limestones, almost only observations in thin sections are available. Due to the insufficient preservation and rather fragmentary character of the material (mostly broken ramose specimens), several taxa of 13 genera identified are listed in open nomenclature.

The bryozoans described are housed in the Paleontological Institute of the Russian Academy of Sciences, Moscow (abbreviated PIN), collection no. 4873.

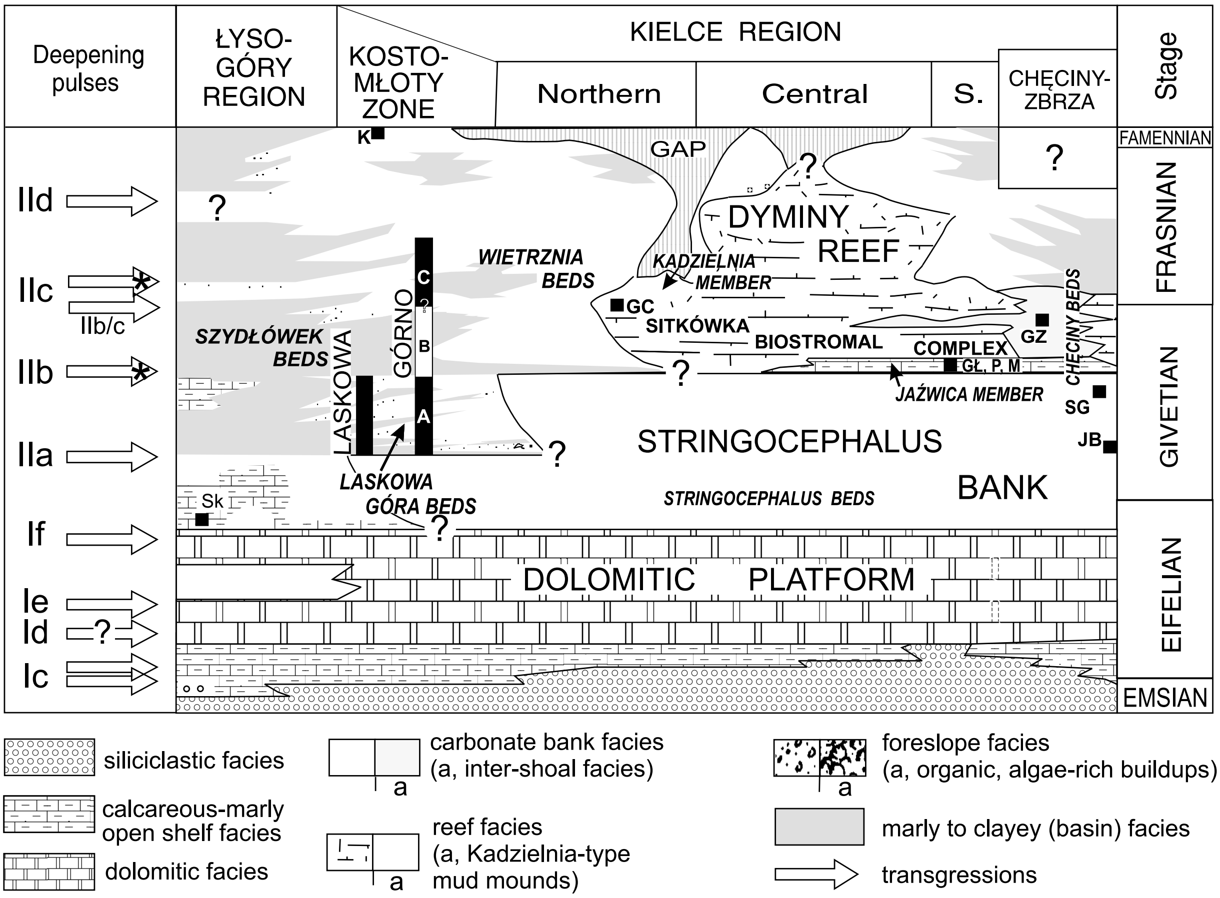

Fig. 2. Position of the bryozoan-bearing sections under study (see Fig. 1B) against developmental stages of the Middle to Late Devonian bank-to-reef complex of the Holy Cross Mountains; stratigraphic-facies cross-section (after Racki 1993: fig. 3, changed) is shown to emphasise eustatic rhythmic control of the depositional pattern and main bryozoan immigrational events in the Kostomłoty basin (asterisked); Ic–IId, transgressive-regressive cycles modified from Johnson et al. (1985); GC, Góra Cmentarna; GŁ, Góra Łgawa; M, Marzysz; P, Posłowice; GZ, Góra Zamkowa; SG, Sowie Górki; JB, Jurkowice-Budy; Sk, Skały; K, Kostomłoty (eastern hill).

Systematics

(I. Morozova and O. Weis)

Order Cystoporida Astrova, 1964
Suborder Fistuliporina Astrova, 1964
Family Fistuliporidae Ulrich, 1882

Fistulipora pavimenta **Bigey, 1988** (Fig. 3A, B).—Two cystoporate colonies were collected at Laskowa Quarry. The upper Givetian age of Holy Cross specimens corresponds well with the type horizon of this species in the upper Givetian of Ferques, northern France (Couderousse Member of Blacourt Formation, Bigey 1988a).

Canutrypa francqana **Bassler, 1952** (Fig. 3C–F).—Middle Frasnian marly-organodetrital Wietrznia Beds (set C at Górno) have provided very abundant zoaria of this species. In addition, this fistuliporid occurs in uppermost Givetian strata at Łgawa Góra (Jaźwica Mbr.) and Chęciny (Zamkowa Góra, lower Chęciny Beds), as well as in the basal Famennian Kostomłoty limestones at Kostomłoty. The species was previously described only from the middle Frasnian strata of France (Ferques Formation, Bassler 1952; Bigey 1988a, b; see also Bassler 1953; Utgaard 1983) and Belgium (Dessilly 1961).

Eridopora orbiculata **(Kiepura, 1973)**.—The cystoporate species occurs in upper Givetian Laskowa Góra Beds at Górno, but was originally described from the uppermost Eifelian Skały Beds at type locality (Łysogóry Region) by Kiepura (1973) with the generic assignment to *Ceramoporella*.

Order Trepostomida Ulrich, 1882
Suborder Halloporina Astrova, 1965
Family Heterotrypidae Ulrich, 1890

Lioclema celebratum **Morozova, 1961** (Fig. 4A–C).—The material from middle Givetian Laskowa Góra Beds at Laskowa Quarry includes 2 colonies. The zooecia examined are conspecific with heterotrypid species from the Kuzbass Givetian (Lebyedansk Beds), Russia (Morozova 1961).

Table 1. Distribution of Devonian bryozoan taxa from Holy Cross Mountains.

Stage	Central Poland, Holy Cross Mts. (see Figs. 1, 2)						
	Upper Givetian			Middle Frasnian			
Locality (lithostratigraphic unit) [conodont zones] Taxon	Kostomłoty, Laskowa Quarry (Laskowa Góra Beds) [Middle *Po. varcus*– *K. disparilis*]	Górno, Józefka Hill, Set A (Laskowa Góra Beds) [?Middle *Po. varcus*– *K. disparilis*]	Other sites* [? Middle *Po. varcus* (J); ?*K. disparilis* to early *M. falsiovalis* (SG, P, GZ)]	Górno, Józefka Hill, Set C (Wietrznia Beds) [*Pa. punctata* ?and adjoining zones]	France (Bigey 1988a, b)	Belgium (Bigey 1988a, b)	Russia (Morozova 1961)
Order Cystoporida							
Fistulipora pavimenta Bigey,1988	+ dominant species	?(*F.* sp.)			Blacourt Fm. Givetian (Middle *Po. varcus*– *K. disparilis*)		
Eridopora orbiculata (Kiepura,1973)		+					
Canutrypa francqana Bassler, 1952			P, GZ (**K)	+ dominant species	Beaulieu Fm. to Ferques Fm. Frasnian (*Pa. punctata*– *Pa. hassi*)	Marlagne Fm. Frasnian (*Pa. hassi*)	
Order Trepostomida							
Lioclema celebratum Morozova, 1961	+	?(*L.* sp.)					Lebedyanka beds [= Altchedat– Isyly Fms.] Givetian–?Frasnian (Middle *Po. varcus*– *M. falsiovalis*)
Atactotoechus polygonius Bigey, 1988	+		?SG		Beaulieu Fm. Frasnian (*Pa. punctata*)		
Eridotrypella arguta sp. nov.				+			
Eridotrypella exserta sp. nov.				+			
Eostenopora nimia sp. nov.		+					
Leptotrypa sp.	+	+	J				
Order Rhabdomesida							
Primorella nitida sp. nov.		+ dominant species					
Primorella indigena sp. nov.				+			
Rhombopora cf. *dispersa* Bigey, 1988			GZ	+	Ferques Fm. Frasnian (*Pa. hassi*)		
Saffordotaxis sp.		+					
Acanthoclema cf. *distilum* Bigey, 1988				+	cf. [Blacourt Fm. Givetian (Middle *Po. varcus*– *K. disparilis*)]		
Orthopora sp.		+					

* Kowala Fm., *Stringocephalus* Beds (Racki 1993): J, Jurkowice-Budy; SG, Sowie Górki; Jaźwica Mbr.: P, Posłowice; lower Chęciny Beds: Z, Góra Zamkowa at Chęciny.
** K, the species present also in the basal Famennian at Kostomłoty.

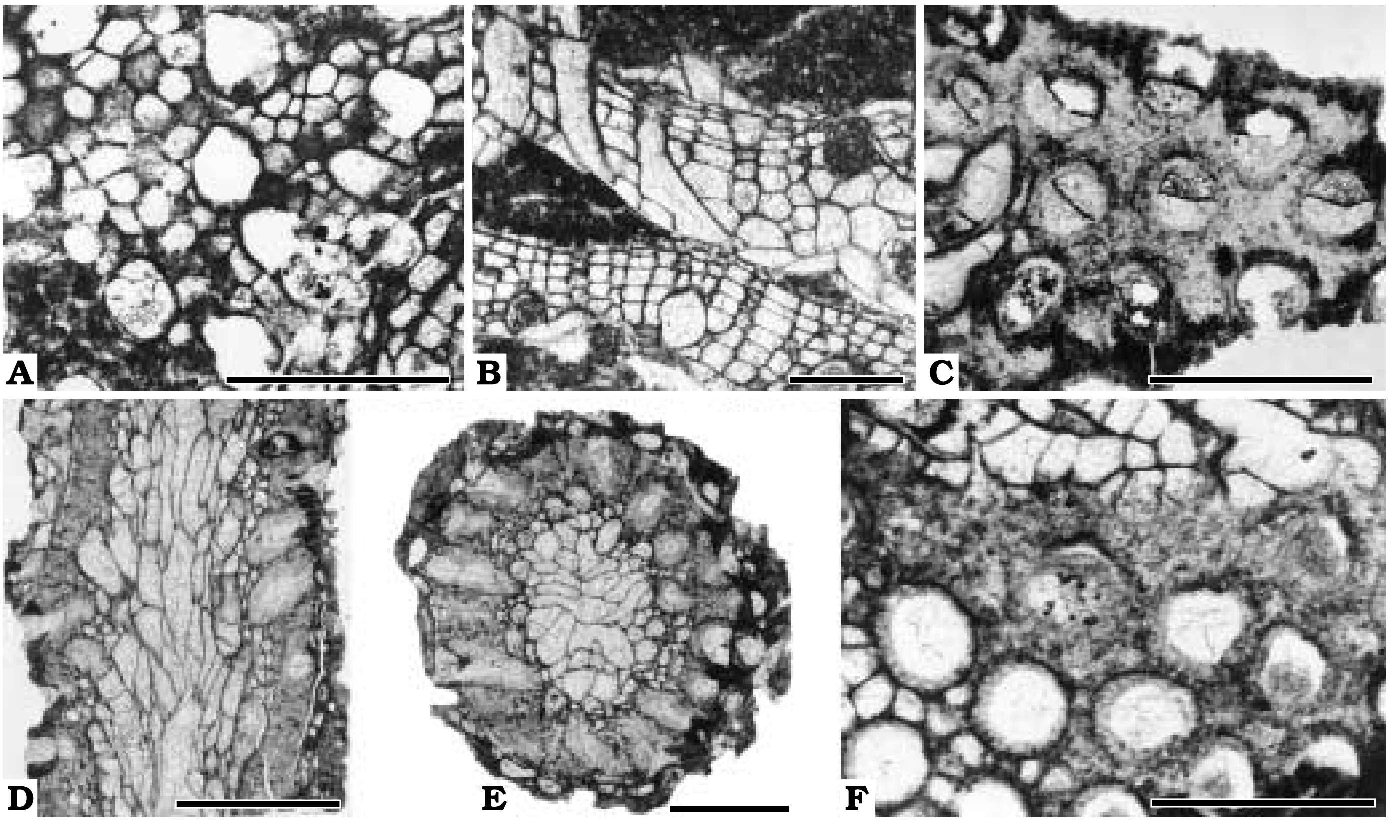

Fig. 3. **A**, **B**. *Fistulipora pavimenta* Bigey, 1988. Shallow tangential (**A**) and longitudinal (**B**) sections of the specimen PIN 4873/23 from Givetian of Laskowa Quarry, Laskowa Góra Beds. **C**–**F**. *Canutrypa francqana* Bassler, 1952. Shallow tangential section (**C**), longitudinal section (**D**), transverse section (**E**), and oblique tangential section with well visible longitudinal section of the autozooecial chambers with diaphragms (**F**) of the specimen PIN 4873/25 from Frasnian of Górno, Józefka Hill, Wietrznia Beds. Scale bars 1 mm.

Suborder Amplexoporina Astrova, 1965
Family Atactotoechidae Duncan, 1939

***Atactotoechus polygonius* Bigey, 1988** (Fig. 4D, E).—Four zoaria were gathered from the upper Givetian Laskowa Góra Beds at Laskowa Quarry. Similar atactotoechid is identified in the thin section from possibly correlative *Stringocephalus* Beds at Sowie Górki. The species was described from the middle Frasnian Beaulieu Formation of Ferques (Bigey 1988a, b).

***Leptotrypa* sp.**—Undeterminable representatives of this common trepostome genus are found in several Givetian localities: Laskowa Góra, Górno (set A) and Jurkowice-Budy (set E). Fragmentary specimens from Górno and Jurkowice-Budy show affinities to *L.*? *crassa* Bigey, 1988, described from the Givetian/Frasnian passage (Cambreséque Mbr. of the Beaulieu Fm.) at Ferques (Bigey 1988a).

Family Eridotrypellidae Morozova, 1961
Genus *Eridotrypella* Duncan, 1939

Type species: *Batostomella obliqua* Ulrich, 1890. Middle Devonian, Hamilton Group; North America (Michigan).

Eridotrypella arguta Morozova and Weis, sp. nov.

Figs. 4F, 5A–C.

Holotype: PIN 4873/5, Fig. 5A–C.

Type locality: Holy Cross Mts (Central Poland), Górno, Józefka Hill (set C), middle Wietrznia Beds; Upper Devonian, middle Frasnian (?*Pa. punctata* Zone).

Derivation of the name: From Latin *argutus*, expressive.

Material.—Five incomplete colonies, 13 thin sections, PIN 4873/5–4873/9.

Diagnosis.—*Eridotrypella arguta* sp. nov. resembles in many characters *E. valentinae* Morozova, 1961 from the Givetian of Russia (Kuzbas), but is distinguished in having fewer diaphragms (1–2 against 4–6) and in having larger diameter of autozooecial apertures (0.18–0.20 mm against 0.11–0.12 mm).

Description.—Colony ramose with branches 1.5–2.5 mm in diameter. Exozone is very thick (0.8–0.9 mm). Diameter of the endozone 0.6–0.7 mm. Zooecial walls in the exozone with transversely laminated structure, not beaded. Thickness of the walls in the exozone 0.02–0.05 mm. Endozonal walls are about 0.015 mm thick. Autozooecia curve gently into the exozone and turn to the surface at an acute angle. Diaphragms thin, rare, one to two per autozooecium located only in the exozone. Autozooecial apertures polygonal, 0.18–0.20 mm in diameter, 7 or 8 in 2 mm, rarely 9. Distance between neighbouring apertural centers both longitudinally and diagonally 0.21–0.27 mm. Exilazooecia are short, very rare and

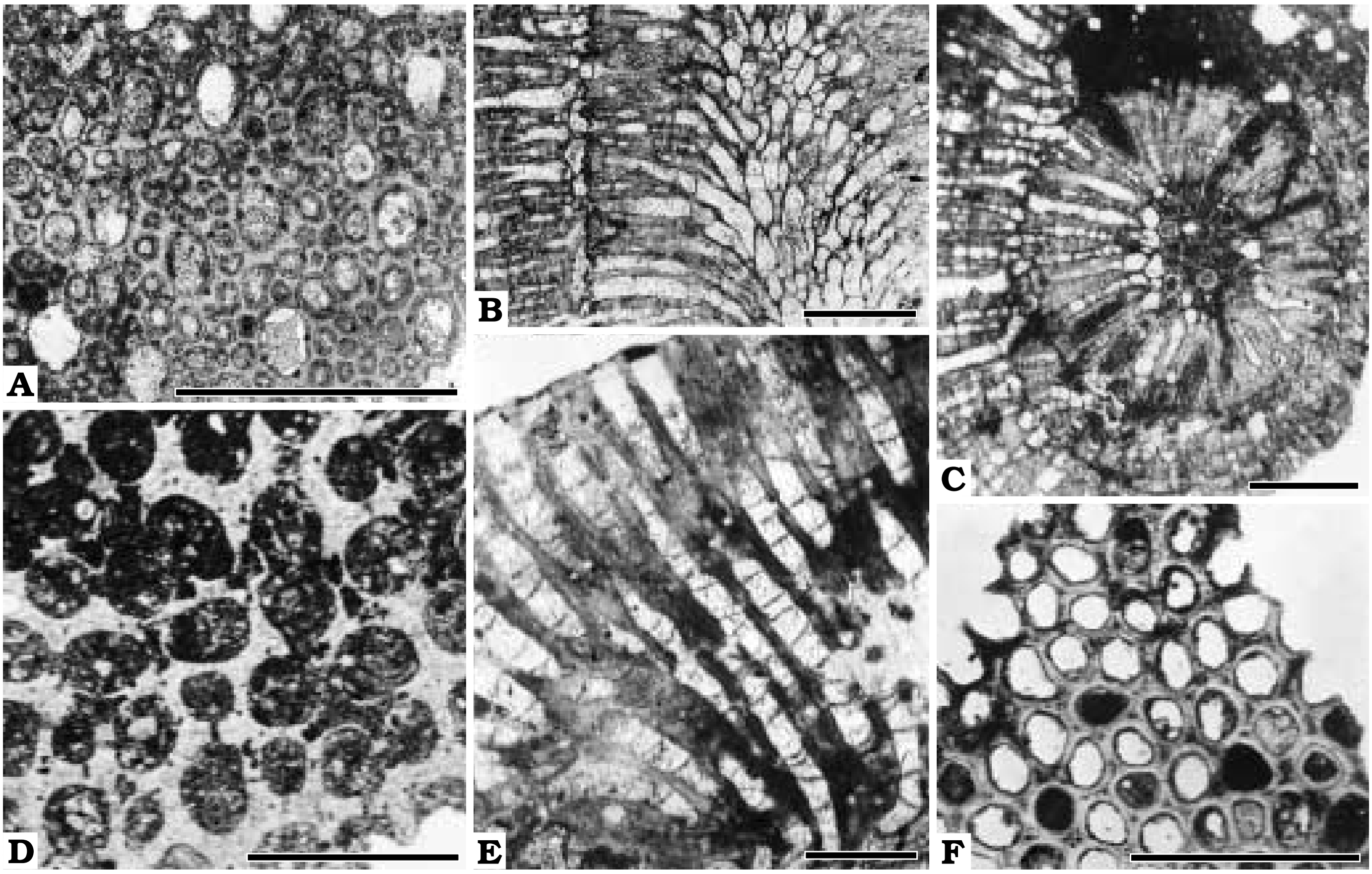

Fig. 4. **A**–**C**. *Lioclema celebratum* Morozova, 1961. Tangential section (**A**), longitudinal section (**B**), and transverse section (**C**) of the specimen PIN 4873/41 from Givetian of Laskowa Quarry, Laskowa Góra Beds. **D**, **E**. *Atactotoechus polygonius* Bigey, 1988. Tangential section (**D**), longitudinal section (**E**) of the specimen PIN 4873/43 from Givetian of Laskowa Quarry, Laskowa Góra Beds. **F**. *Eridotrypella arguta* Morozova and Weis, sp. nov. Tangential section of the paratype PIN 4873/6 from Frasnian of Górno, Józefka Hill, Wietrznia Beds. Scale bars 1 mm.

small, of subcircular outline. Diameter of the exilazooecial apertures 0.04–0.06 mm. Numerous small pores (capillaries) about 0.003 mm in diameter pierce all walls in the exozone and form small accumulations around the stellatopores at junctions of the zooecial walls.

Remarks.—Dense accumulations of capillaries on the colony surface (stellatopores) surrounding each autozooecial aperture are characteristic of the holotype of *Eridotrypella arguta* and other species of this genus. Many authors (e.g., Duncan 1939; Morozova 1961; Astrova 1978) assumed them erroneously to be acanthopores (acanthozooecia) which, in fact, lack them in this genus, as well as *Eostenopora*, the other genus of the family Eridotrypellidae. Therefore, diagnoses of these generashould be revised.

Occurrence.—Only the type locality.

Eridotrypella exserta Morozova and Weis, sp. nov.

Fig. 5D–H.

Holotype: PIN 4873/20, Fig. 5D–H.

Type locality: Holy Cross Mts (Central Poland), Górno, Józefka Hill (set C of Racki 1993), middle Wietrznia Beds; Upper Devonian, middle Frasnian (?*Pa. punctata* Zone).

Derivation of the name: From Latin *exsertus*, prominent.

Material.—Two colonies, 6 thin sections, PIN 4873/20, 4873/21.

Diagnosis.—*E. exserta* sp. nov. differs from the closest *E. granulosa* Morozova, 1955 in having largest autozooecial apertures (0.18–0.22 mm in diameter instead of 0.10–0.20 mm in *E. granulosa*) and 5 apertures per 2 mm along colony and 6–6.5 diagonally instead of 8–9 apertures along colony and 10–11 diagonally in *E. granulosa*. Besides, the new species differs in having different size and form in the tangential section of the exilazooecial apertures forming small accumulations in maculae, and in having smaller capillaries (0.001–0.002 mm in diameter instead of 0.004–0.005 mm in *E. granulosa*).

Description.—Colony thin, ramose. Branches circular or slightly oval in transverse section, 1.7–2.4 mm in diameter. Exozone thickness 0.7–0.8 mm. Endozone very narrow, generally constituting one quarter or less of the colony diameter. Walls of the autozooecia in the endozone crenulated and gradually thickenning from beginning of endozone to outward. Thickness of the endozone walls 0.015 mm, that of the zooecial walls in exozone varies between 0.03 mm to 0.06 mm.

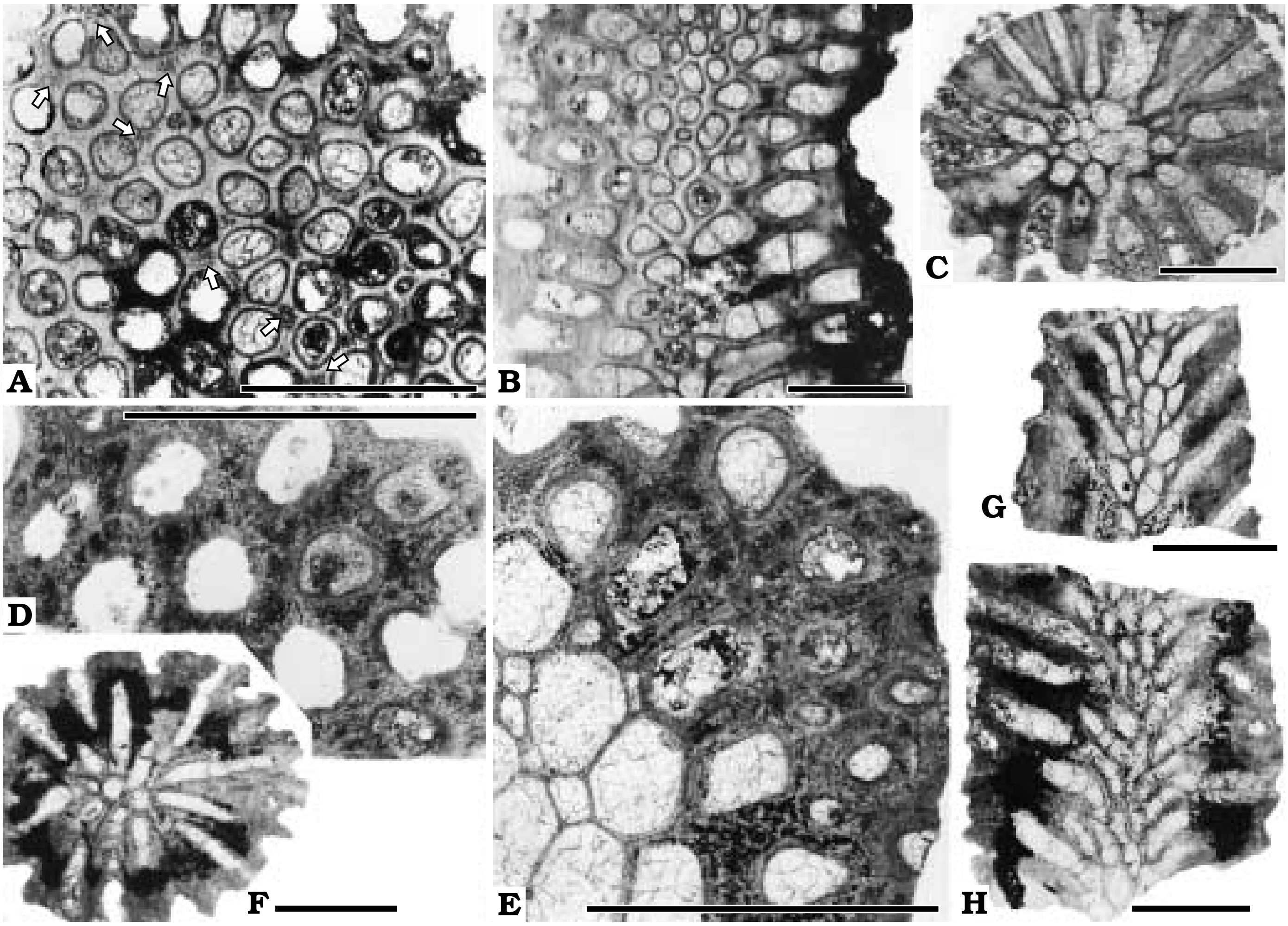

Fig. 5. **A**–**C**. *Eridotrypella arguta* Morozova and Weis, sp. nov. Tangential section with capillaries indicated with arrows (**A**), oblique longitudinal section (**B**), transverse section (**C**) of the holotype PIN 4873/5 from Frasnian of Górno, Józefka Hill, Wietrznia Beds. **D**–**H**. *Eridotrypella exserta* Morozova and Weis, sp. nov. Tangential section (**D**), oblique tangential section with exilazooecia forming small accumulations in macula (**E**), transverse section of the main stem (**F**), longitudinal section of a lateral branch (**G**), longitudinal section of the main stem (**H**) of the holotype PIN 4873/20 from Frasnian of Górno, Józefka Hill, Wietrznia Beds. Scale bars 1 mm.

Autozooecial chambers are with complete straight or curve diaphragms developed in the endozone (1–2 diaphragms) and exozone (4–6). Autozooecial apertures arranged in oblique rows. Their shape is slightly oval or irregularly circular. The length of the oval apertures ranges from 0.18 to 0.22 mm, and the width from 0.17 to 0.18 mm. Diameter of almost circular apertures is 0.20–0.22 mm. Distance between neighbouring apertural centers along colony 0.27–0.30 mm, diagonally 0.26–0.28 mm. There are about 5 apertures per 2 mm along colony and 6–6.5 diagonally. Exilazooecial apertures are irregularly distributed forming small accumulations in maculae (Fig. 5E), sometimes 1–2 exilazooecia meet near autozooecia. Outline of the exilazooecium apertures subcircular or oval near the colony surface, in deep tangential sections they become subangular. Diameters of the subcircular exilazooecial apertures 0.02–0.06 mm; the oval apertures are 0.02–0.03 mm long and 0.15 mm wide. Around each autozooecial and exilazooecial apertures stellatopores 5–6 are developed being about 0.02–0.03 mm in diameter. Numerous capillaries surround the stellatopores. Diameter of the capillaries 0.005 mm.

Remarks.—*Eridotrypella exserta* sp. nov. is similar only to Russian *Eridotrypella spinulosa* (Morozova,1955), described from the upper Frasnian of Kuzbass (Morozova 1955: 784–785, fig. 1). Both species have delicate colonies with thick exozone and very narrow endozone and numerous diaphragms in autozooecia.

Occurrence.—Only the type locality.

Genus *Eostenopora* Duncan, 1939

Type species: *Eostenopora picta* Duncan, 1939. Middle Devonian, Givetian, Traverse Group of North America (Michigan).

Eostenopora nimia Morozova and Weis, sp. nov.

Fig. 6A–C.

Holotype: PIN 4873/1, Fig. 6A–C.

Type locality: Holy Cross Mts (Central Poland), Górno, Józefka Hill (set A of Racki 1993), Laskowa Góra Beds; Middle Devonian, upper Givetian (?Middle *Po. varcus* to *K. disparilis* zones).

Derivation of the name: From Latin *nimius*, excessive.

Material.—Four incomplete colonies, 8 thin sections, PIN 4873/1–4873/4.

Diagnosis.—*Eostenopora nimia* sp. nov. resembles *E. primiformis* Duncan, 1939 from the Traverse Group of Michigan in having an incrusting colony, but is distinguished by the thick walls in exozone, wide peristomes in autozooecial and exilazooecial apertures, transversely laminated structure of the zooecial walls and by more abundant acanthostyles.

Description.—Colony encrusting a crinoid column(?). Maximum thickness of laminae 0.50 mm. The endozone is well distinguishable from the exozone. The thickness of the exozone 0.38–0.46 mm, width of the endozone—0.06–0.11 mm. Zooecial walls in the exozone very thick—0.08–0.15 mm with transversely laminated structure. Zooecial walls in the endozone 0.01 mm thick. Autozooecial chambers short. Only one or two straight diaphragms in each autozooecia. Apertures of autozooecia subcircular with thick peristome. The thickness of the peristome 0.03–0.04 mm. Diameter of the aperture 0.16–0.17 mm. Six apertures per 2 mm measured diagonally, five per 2 mm measured along colony. Distance between neighbouring apertural centers along the colony 0.26–0.32 mm. Apertures of autozooecia on the maculae arranged in irregular rows. They are oval, 0.19–0.22 mm long and 0.008–0.009 mm wide. Exilazooecial apertures with thick walls (0.003 mm) are irregularly distributed. Outline of the exilazooecial apertures is subcircular with diameter 0.02–0.04 mm. Acanthostyles on the zooecial walls occasionally vary from 0.016 to 0.030 mm in diameter. Eight to twelve acanthostyles surround each autozooecial aperture. Exozonal walls near the colony surface are pierced by numerous short pores (capillaries) 0.005–0.006 mm in diameter.

Occurrence.—Only the type locality.

Order Rhabdomesida Astrova and Morozova, 1956
Family Rhomboporidae Simpson, 1895
Genus *Primorella* Romantchuk and Kiseleva, 1968

Type species: *Primorella polita* Romantchuk and Kiseleva, 1968. Upper Permian; Russia, Far Eastern region.

Remarks.—Two new Holy Cross rhabdomesid species are first Devonian representatives of *Primorella*, known till only from Carboniferous–Permian strata.

Primorella nitida Morozova and Weis, sp. nov.

Fig. 6D–G.

Holotype: PIN 4873/11, Fig. 6D–F.

Type locality: Holy Cross Mts (Central Poland), Górno, Józefka Hill (set A of Racki 1993), Laskowa Góra Beds; Middle Devonian, upper Givetian (?Middle *Po. varcus* to *K. disparilis* zones).

Derivation of the name: From Latin *nitidus*, elegant, fine.

Material.—Five colonies, 15 thin sections, PIN 4873/11–4873/15.

Diagnosis.—This species is similar to stratigraphically younger *Primorella indigena* sp. nov. in most characters, but distinctly differs in the smaller diameter of colony (0.9–1 mm instead 1.7–2 mm instead of in *P. indigena*) and in thinner zooecial walls in the exozone. Autozooecial apertures of *P. nitida* are largely oval (instead of subcircular in *P. indigena*), whilst stellatopores are more numerous (7–12 around the apertures, instead of 6–9).

Description.—Colony thin, ramose. Diameter of branches 0.9–1 mm; thickness of exozone 0.26–0.35 mm, width of endozone about 0.40–0.45 mm. The spirally budding autozooecia gently bend outward from the central axis. The autozooecial chambers are long and tubular, with 2–4 diaphragms in each autozooecium. Diaphragms complete, straight or concave. Zooecial walls in the endozone 0.007–0.01 mm thick, the thickness of zooecial walls in the exozone 0.11–0.13 mm. Apertures arranged in regular longitudinal series and cross diagonal rows. Aperture outlines oval, averaging 0.17–0.20 mm in length, and 0.08–0.10 mm in width. In 2 mm there are 6–6.5 apertures along the colony and 8 diagonally across the colony. Distance between neighbouring apertural centers along colony 0.35–0.45 mm, diagonally 0.20–0.24 mm. Numerous stellatopores (actinotostyles of the American authors [Blake 1983]) and small pores surround the apertures and pierce all walls in the exozone. Diameter of stellatopores 0.01–0.03 mm. Seven to twelve stellatopores developed as a chain around each autozooecial aperture. Diameter of capillaries 0.003–0.004 mm.

Occurrence.—Only the type locality.

Primorella indigena Morozova and Weis, sp. nov.

Fig. 6H–J.

Holotype: PIN 4873/16, Fig. 6H–J.

Type locality: Holy Cross Mts (Central Poland), Górno, Józefka Hill (set C of Racki 1993), middle Wietrznia Beds; Upper Devonian, middle Frasnian (*Pa. punctata* Zone).

Derivation of the name: From Latin *indigenus*, local.

Material.—Three colonies, 8 thin sections, PIN 4873/16–4873/18.

Diagnosis.—This Frasnian species differs from *P. nitida* sp. nov. in its larger measurements, namely in the diameter of colony (1.7–2 mm in *P. indigena*, 0.9–1 mm in *P. nitida*), and also in thicker zooecial walls in the exozone. Most of autozooecial apertures of *P. indigena* are subcircular (oval in *P. nitida*) and arranged in irregular longitudinal series. The stellatopores are not so abundant (6–9 around the apertures, instead of 7–12).

Description.—Colony thin, ramose. Diameter of branches 1.70–2 mm, thickness of exozone 0.50–0.52 mm, width of endozone 0.65–0.70 mm. Autozooecial tubes curve gently from mesotheca outward at an angle of about 45°. Autozooecial chambers are with 3–5 diaphragms in the exozone.

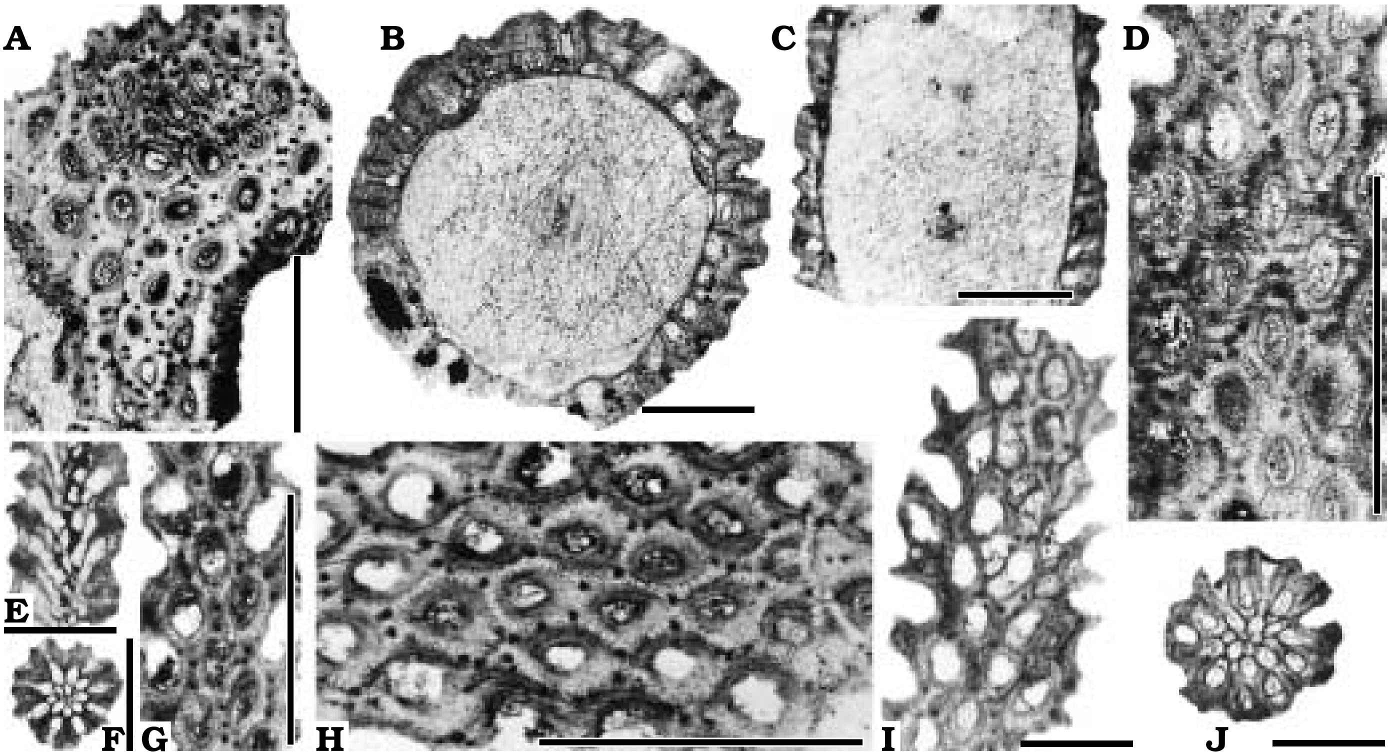

Fig. 6. **A**–**C**. *Eostenopora nimia* Morozova and Weis, sp. nov. Tangential section (**A**), transverse section (**B**), longitudinal section (**C**) of the holotype PIN 4873/1 from Givetian of Górno, Józefka Hill, Laskowa Góra Beds. **D**–**G**. *Primorella nitida* Morozova and Weis, sp. nov. Tangential section (**D**), longitudinal section (**E**), transverse section (**F**) of the holotype PIN 4873/11 from Givetian of Górno, Józefka Hill, Laskowa Góra Beds, tangential section (**G**) of the paratype PIN 4873/12; locality and age are the same. **H**–**J**. *Primorella indigena* Morozova and Weis, sp. nov. Tangential section (**H**), longitudinal section (**I**), transverse section (**J**) of the holotype PIN 4873/16 from Frasnian of Górno, Józefka Hill, Wietrznia Beds. Scale bars 1 mm.

Diaphragms complete, sometimes concave. Zooecial walls are thin in endozone (0.01 mm) becoming rapidly thickened in exozone (0.20–0.25 mm). Aperture outline subcircular, rarely oval. Diameter of circular apertures 0.10–0.12 mm. The length of oval apertures 0.13–0.14 mm, the width—0.10–0.11 mm. In 2 mm there are 5 apertures along colony and 8 diagonally. Distance between neighbouring apertural centers along colony 0.4–0.5 mm, diagonally 0.25–0.3 mm. Six to nine stellatopores with a diameter of about 0.01–0.03 mm are present around each autozooecial aperture. Numerous capillaries surround the stellatopores and pierce all walls in exozone. Diameter of capillaries 0.005 mm.

Occurrence.—Only the type locality.

***Rhombopora* cf. *dispersa* Bigey, 1988**.—Poorly-preserved ramose zoaria, very close to the French species from middle Frasnian Ferques Formation (Bigey 1988a, b), occur in the uppermost Givetian at Chęciny (Zamkowa Góra, lower Chęciny Beds), as well as in middle Frasnian strata at Górno (Wietrznia Beds).

***Saffordotaxis* sp**.—Representatives of this rhabdomesid genus are found exclusively in the upper Givetian bryozoan association from Górno (Laskowa Góra Beds).

***Acanthoclema* cf. *distilum* Bigey, 1988**.—Zoaria resembling *A. distilum* from the Blacourt Formation at Ferques (Bigey 1988a) occur in the upper Givetian strata at Górno (Laskowa Góra Beds).

***Orthopora* sp**.—This rhabdomesid genus is rarely represented in diverse upper Givetian bryozoan association from Górno (Laskowa Góra Beds).

Discussion

Twelve species have been identified, representing 13 bryozoan genera belonging to four families and three orders (Table 1) (severely fragmented fenestellids from Górno are omitted). All bryozoans have been recovered from two time intervals of the Devonian deposits: late Givetian and middle Frasnian. In general biogeographical terms, the bryozoan associations are marked by dominance of cystoporids and thin-ramose rhabdomesids, whilst coeval faunas of other regions (Transcaucasia, South Siberia, Northern America, China) contain far more abundant fenestellids and trepostomes (see e.g., Naimark et al. 1999). Most species are close or common to species from the more or less coeval deposits in northern France. This is indicative that at that time there existed a good communication between these two open marine basins on southern Laurussian shelf, and that the environmental conditions in which bryozoans lived were similar.

Additionally, it should be noted that *Lioclema celebratum*, as well as *Leptotrypa rhombocella* Morozova, 1961, identified in the uppermost Givetian sites of Kielce region (Łgawa Góra, Marzysz, Zamkowa Góra), were known previously exclusively from the Givetian–Frasnian deposits in South Siberia (Kuzbass; see Morozova, 1961). Also *Fistulipora pavimenta*, common in the Laskowa Góra Beds at Laskowa, shows close affinities with the *F. volhynica* Dunaeva, 1970, and both new Frasnian eridotrypellid species from Górno are similar only to Kuzbass trepostomes. An endemic aspect is also recognizable especially among rhabdomesids, because two oldest species of the Late Palaeozoic genus *Primorella* are described herein. As shown by Naimark et al. (1999), Palaeozoic centers of bryozoan diversification correspond chiefly to regions characterized by favorable life conditions, especially where eurytopic fenestellids are less important component. Therefore, a biogeographically transitional aspect of the Holy Cross faunas is confirmed to some extent (Racki 1988), even if dispersal routes and links with eustatic transgressive–regressive cyclicity remain still in question (see also discussion in Bigey 1988a: 298).

During IIa and IIc transgressive events (*sensu* Johnson et al. 1985; see Fig. 2), drowning of the northern part of Kielce platform is clearly paired with two-step colonisation of foreslope environments by various bryozoan baffle associations, partly revealing links with stratigraphicaly older Łysogóry faunas among the most abundant fistuliporids at Laskowa (inter-regional immigrations of Racki 1988). Eastward, the approximately correlative fauna at Górno were dominated by the rhabdomesid *Primorella nitida.* The fairly diverse Frasnian fauna is known exclusively from the Górno succession and absent in the coeval Wietrznia Beds at the fossiliferous type locality in Kielce; this unique association is distinguished by high abundance of *Canutrypa franoqana*, the species limited in distribution to Western and Central Europe. Various trepostomates, especially rhabdomesids, and fenestellids were probably more widely distributed in the Kielce bank-to-reef habitats, especially in the open-shelf muddy biotopes of Jaźwica Mbr. (Racki 1993: 116–118), but their specific position is only partly clarified herein. Even very rich bioherm-dwelling benthos of the early Frasnian Kadzielnia mud mound includes few bryozoans (see summary in Racki 1993: 130), although large colonies of *Rectifenestella* occur at Góra Cmentarna in Kielce (also Gürich 1896). Apparently, gentle slope (ramp-style) low-energy muddy habitats of the Kostomłoty basin were the most convenient life setting for bryozoan thriving in the shallow carbonate shelf under study, comparable e.g., to Silurian benthic environments within the Gotland reef complex (see Brood 1975). The bryozoans under study are associated with very diverse brachiopod-crinoid-coral biotas of late Givetian tabulate thickets (locally mud mounds) dominated by *Coenites* and alveolitid-chaetidid faunas (Laskowa Quarry; Racki et al. 1985) or by *Alveolitella fecunda* (Józefka Hill; see Nowiński 1993). Concerning the middle Frasnian fauna from Górno, the fragmentarily still known brachiopod-crinoid-bryozoan (*Biernatella*-dominated) assemblage (see Baliński 1995) might include some redeposited, reef-dwelling elements as suggested by bryozoan co-occurrence with broken laminar and dendroid stromatoporoids. In contrary, argillaceous Szydłówek Beds, corresponding exactly to the Middle–Upper Devonian transition, record a major (in the regional perspective; Racki et al. 1985; Racki 1993) IIb deepening pulse, evidently interrupting development of bryozoan-rich benthic biotas.

Later Frasnian and particularly early Famennian bryozoan record is rather poor worldwide (see review in Bigey 1988b), and these fossils are almost lacking through the key interval in the Dyminy Reef complex of the Holy Cross Mts (?sporadic rhabdomesids and fenestellids only). This scarcity is well exemplified also by detrital (algae-rich) upper Frasnian to basal Famennian Kostomłoty limestones of the facies zone under study (see Casier et al. 2000), where, however, a single zoarium of *Canutrypa francqana* is discovered in thin section. In general, the Frasnian–Famennian collapse of reef ecosystems is recognized as not very catastrophic among stress-resistant colonial bryozoans (in contrast to "solitary" lophophorate brachiopods; Afanasjeva and Morozova 1995; see also Bigey 1988b; Xia 1997; Webster et al. 1998); for example, bryozoans belong to important builders of calcimicrobe-dominated earliest Famennian reefs in the Canning basin, northwestern Australia (Wood 2000). In contrast, the late Givetian extinction ranks by Horowitz et al. (1996) as the largest bryozoan turning point in the Phanerozoic. Thus, the established regional replacement of locally abundant and diverse Givetian bank faunas by overall impoverished Frasnian reef-related associations over northern periphery of Kielce the platform facies, i.e., regional disappearance of at least 8 from 11 species (see Table 1), largely corresponds to the Givetian bryozoan acme followed by a major extinction event in evolutionary history of the phylum.

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